

## LETTER

# Phenology and flowering overlap drive specialisation in plant–pollinator networks

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**Abstract**

Variation in dietary specialisation stems from fundamental interactions between species and their environment. Consequently, understanding the drivers of this variation is key to understanding ecological and evolutionary processes. Dietary specialisation in wild bees has received attention due to their close mutualistic dependence on plants, and because both groups are threatened by biodiversity loss. Many principles governing pollinator specialisation have been identified, but they remain largely unvalidated. Organismal phenology has the potential to structure realised specialisation by determining concurrent resource availability and pollinator foraging activity. We evaluate this principle using mechanistic models of adaptive foraging in pollinators within plant–pollinator networks. While temporal resource overlap has little impact on specialisation in pollinators with extended flight periods, reduced overlap increases specialisation as pollinator flight periods decrease. These results are corroborated empirically using pollen load data taken from bees with shorter and longer flight periods across environments with high and low temporal resource overlap.

**KEYWORDS**

adaptive foraging, diet specialisation, phenology, pollen, seasonality, temporal resource density

## INTRODUCTION

The dietary specialisation of an organism sits at the nexus of numerous fundamental processes in ecology and evolutionary biology. Dietary specialisation helps define organismal niches (Kartzinel et al., 2015), mediates migration and dispersal potential (Bommarco et al., 2010; Boyle et al., 2011), shapes inter- and intraspecific competition (deVries, 2017; Svanbäck & Bolnik, 2007), influences species persistence in the face of environmental disturbance (Wood et al., 2019) and can affect the rates of speciation and extinction (Thompson, 1998).

Even the simple assembly of the collection of organisms' dietary ranges in a community defines one of the major concepts in ecology, the food web. Therefore, identifying the drivers influencing dietary specialisation provides fundamental steps towards understanding a multitude of essential biological questions.

Much of the progress in understanding dietary specialisation in consumers comes from studies of herbivory (Kartzinel et al., 2015), particularly on insects (Forister et al., 2015). Using wild bees and plant–pollinator networks as our study system, we extend the scope of those studies to include mutualistic interactions. Mutualisms are ubiquitous ecological interactions in which participant species benefit each other (Bronstein, 1994). Pollination, therefore, differs from other insect herbivory

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because of the reproductive benefit offered to both consumer and consumed species. Bees depend on removing pollen from flowers to rear their offspring, providing a pollination service at the same time (Westerkamp, 1996). Pollination is also of particular interest given its role in supporting terrestrial biodiversity (Biesmeijer et al., 2006) and agricultural output (Garibaldi et al., 2013), a role threatened by widespread declines in both pollinators and insect-pollinated plants (Biesmeijer et al., 2006; Burkle et al., 2013). Some studies have investigated 'specialisation' in plant–pollinator networks, but based on floral visitation rather than the actual interaction of pollen collection (Dorado et al., 2011; King et al., 2013). Where pollen collection has been measured, it has often been in the context of building networks of pollen transfer (e.g. Alarón, 2010; Lopezaraiza-Mikel et al., 2007), but these studies do not concurrently investigate or clarify the dietary niche of the pollinators themselves. In contrast, the pollen diets of wild bee pollinators have frequently been quantified, but often without a focus on the ecological drivers of dietary specialisation (e.g. Wood & Roberts, 2018). This knowledge gap emphasises the need to investigate the biological processes explaining the realised specialisation of pollinators within plant–pollinator networks that account for the actual interaction of pollen collection by pollinators.

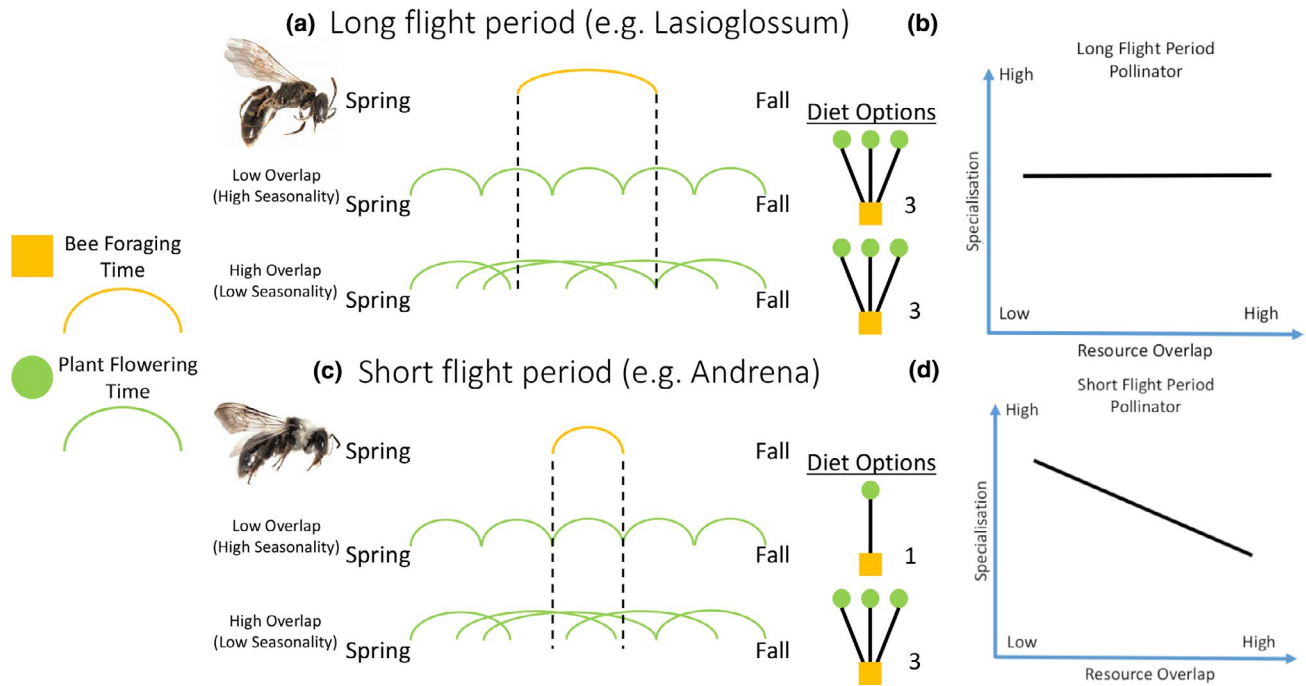
Research into insect herbivores has largely focused on how adaptation to plant traits and defences drives consumer concentration on specific phylogenetically related resources (Ali & Agrawal, 2012; Hunter, 2016). Though the imposition of a taxonomic hierarchy does not fully capture all similarities and distances between host plants (Fordyce et al., 2016), grouping host plants by botanical family allows for broad comparisons to be made between more and less generalised species (Forister et al., 2015). In addition to phylogenetically inherent plant traits that are important for the dietary specialisation of herbivores, other drivers have been identified for consumers more generally (MacArthur & Pianka, 1966; Waser et al., 1996, see Table 1, Appendix S1.1). Here, we expand on the fundamental effect of resource density on a consumer's dietary specialisation (MacArthur & Pianka, 1966), not in a spatial context, but temporally. This resource density is important in its interaction with consumer

phenology. For long-lived organisms (e.g. predatory vertebrates), opportunities to access a single resource type principally depend on the resource's spatial distribution. If a single resource type is physically dense, then a predator can specialise on it without needing to turn to alternatives, whereas if it is patchily distributed then a strategy of specialisation is less optimal. However, for a comparatively short-lived organism like a bee whose adult flight period (its *de facto* lifespan in the context of resource gathering for reproductive investment) can be measured in days, the distribution of a resource type in time is also a critically important determinant of accessibility. A plant species that flowers for 30 days is a *de facto* dense, continuously available resource for a co-occurring bee species whose flight period lasts for only 25 days. However, this same plant species that flowers for 30 days can be considered to be sparse and patchily distributed for a separate bee species which flies for 90 days. The temporal pattern of flowering can therefore be considered analogous to resource density, variations in which will be acutely experienced by short-lived organisms. These ideas have proven influential (e.g. CaraDonna et al., 2017; Robinson & Wilson, 1998) and aspects of phenology have been implemented in network models for the sake of other ecological questions (e.g. Encinas-Viso et al., 2012), but direct theoretical and empirical validation is required to solidify our understanding of phenological drivers of diet breadth.

Expanding upon this idea of temporal density, we hypothesise that the degree of temporal overlap in the availability of different resources (flowering overlap among co-occurring plant species) in combination with the fundamental life-history phenologies of bees (adult flight period) can influence realised dietary specialisation (i.e. their actual choices made under real-world conditions). Applied to plant–pollinator systems, we hypothesise that increased flowering overlap will reduce the dietary specialisation (i.e. increase generalisation) of pollinators with short flight periods, but not necessarily those with long flight periods (Figure 1). Pollinators with short flight periods will experience markedly different resource availability based on the degree of temporal overlap of co-flowering species. High flowering overlap will allow pollinators with short flight periods access to

**TABLE 1** Factors favouring specialisation in foraging as detailed in MacArthur and Pianka (1966) and their corresponding construction in Waser et al.'s (1996) study on factors favouring generalisation in foraging. The third column describes the common factor in each treatment. The factor noted in green highlights the work which helped inspire our study

Drivers of specialized diet (MacArthur and Pianka 1966)	Drivers of generalized diet (Waser et al. 1996)	Common factor
Greater density of a specific resource	Long foraging period relative to availability of specific resources	Resource density, either spatially or temporally
Travel is easy for forager	Travel is costly for forager	Cost associated with travelling to resources
High degree of distinction between resource options	High degree of similarity between resource options	Inherent differences in resource quality
Increased difficulty in resource procurement and utilisation	Minor constraints of behaviour and morphology	Inherent difficulty in accessing different resources



**FIGURE 1** Graphical diagram of our hypothesis. Our hypothesis stems from the temporal overlap of flowering resources available to pollinators. Highly seasonal delimitations between different flowering populations create low levels of temporal overlap among different flowering resources. On the other hand, fewer seasonal delimitations between different flowering populations create higher levels of temporal overlap among different flowering resources. (a) In long flight periods pollinators (e.g. *Lasioglossum*), differing levels of temporal resource overlap have a weaker average effect on the degree of diet options available to the pollinator. (b) This is predicted to lead to a non-significant relationship between overlap and specialisation among long flight periods pollinators. (c) In short flight periods pollinators (e.g. *Andrena*), low and high temporal resource overlap can limit or expand pollinator diet options respectively. (d) This is predicted to lead to a significant relationship between overlap and specialisation in short flight periods pollinators

a greater number of options available concurrently while low overlap will restrict options. Pollinators with long flight periods are nominally less constricted by the temporal overlap of co-occurring resources, theoretically having access to the same number of options over the course of their flight periods regardless of the degree of overlap on average (Figure 1). Importantly, our hypothesis does not indicate that flight period will necessarily correspond with and predict being more or less specialised *ceteris paribus*. Instead, it describes how temporal resource overlap will influence dietary specialisation as a function of pollinators' flight periods when considered as an average response across a community.

We employed a multifaceted approach to test our hypothesis. First, we leverage advances in modelling adaptive foraging in ecological networks (Valdovinos et al., 2013, 2016) to directly address the phenological mechanism driving dietary specialisation across different pollinator flight periods. Second, we utilise our intercontinental pollen load data set of bees with a short flight period (genus *Andrena*) and bees with a long flight period (genus *Lasioglossum*) from both a highly seasonal and a less seasonal environment which function as low and high temporal resource overlap treatments, respectively, to empirically test the effects of overlap. Although the modelling and empirical approaches differ quantitatively, qualitatively comparing their outputs allows for

independent assessments of the mechanism proposed in our hypothesis (Figure 1).

## METHODS

### Model development

Plant–pollinator network models have two major components, the network structure and the dynamics that occur on those networks. The networks used in this study were grouped into size classes with plant–pollinator ratio based on an empirical pollination network (see Appendix S1.2). Before simulations, networks were fully connected to give each pollinator population the maximum within-model range of dietary options without a priori restrictions (Figure S1). Namely, the adjacency matrices were filled entirely with 1s, indicating all potential interactions are initially considered possible (see Appendix S1.2). The realised interactions within simulations emerge from the population, mutualistic and adaptive foraging dynamics occurring on the network structure which were implemented based on existing work (Valdovinos et al., 2013, 2016). In summary, the model mechanistically models pollination as a consumer–resource interaction by separately accounting for vegetative density and floral rewards consumed by pollinators.

The model's time-dependent variables track the adaptive dynamics of each plant species' population dynamics ( $p(t)_i$ ), each animal pollinator species' population dynamics ( $a(t)_j$ ), each plant species' pool of floral rewards ( $R(t)_i$ ) and the adaptive dynamics of the per capita foraging effort preferences of each pollinator species  $j$  for each plant species  $i$  ( $\alpha(t)_{ij}$ ; henceforth referred to as foraging effort). Visits of pollinator  $j$  to plant  $i$  ( $V_{ij}$ ) are consumer interactions between pollinator  $j$  and plant  $i$ 's floral rewards. These visits ( $V_{ij}$ ) result in mutual reproductive benefit, and pollinator effort for any given plant changes dependent upon that benefit. Specifically, pollinator  $j$ 's foraging effort on plant  $i$  ( $\alpha_{ij}$ ) increases whenever pollinator  $j$ 's reward intake from plant  $i$ ,  $f_{ij}(R_i)$ , is higher than its average reward intake from all the plants (subset  $P_j$ ) constituting its diet,  $\sum_{k \in P_j} \alpha_{kj} f_{kj}(R_k)$ . Please see the full description of the underlying dynamic model in Appendix S1.2.

Temporal plasticity in network connectivity was implemented by incorporating time-dependent phenology functions to modify the rates controlling interactions between plants and pollinators in the network. These functions are formed using modified sinusoidal wave functions which produce unique phenologies for every plant  $i$  ( $T_{p_i}$ ) and animal pollinator  $j$  ( $T_{a_j}$ ). In flowering plant species, the phenology function  $T_{p_i}$  (see Appendix S1.3) modifies the phenology of floral reward production ( $R_i$ ). The  $T_{p_i}$  function controls the flowering of plant  $i$ , such that plant  $i$  only produces floral rewards when  $T_{p_i} > 0$  (the flowering period), otherwise reward production is 0 during interceding periods of inactivity we call 'break periods'. Similarly, in animal pollinators, all visitation rates ( $V$ ) are modified by the phenology function  $T_{a_j}$  such that pollinators are only foraging during their flight period and not during interceding break periods (see Appendix S1.3). The  $T_{a_j}$  function also modifies  $\alpha_{ij}$  such that foraging effort preferences only change during active flight periods. With this framework, any active flying pollinator and flowering plant can only potentially interact during phenological co-occurrence (Figure 2). Note that even overlapping phenologies between pollinators and plants only produce potential interactions as adaptive foraging drives pollinator foraging choices among possible resources.

Scaling up this framework to multiple interactions introduces temporal plasticity in network topology through organismal phenology as unique potential interactions activate and deactivate across time (Figure S5). The phenology functions ( $T_{p_i}$  &  $T_{a_j}$ ) were designed to be sufficiently malleable with only simple user inputs that facilitate direct control over the temporal availability of specific resources and the activity patterns of the animal pollinators over time in simulations (see Appendix S1.4, Figure S1-S5). These inputs are the duration of flowering/foraging periods and a parameter dictating the length of time interceding between subsequent periods

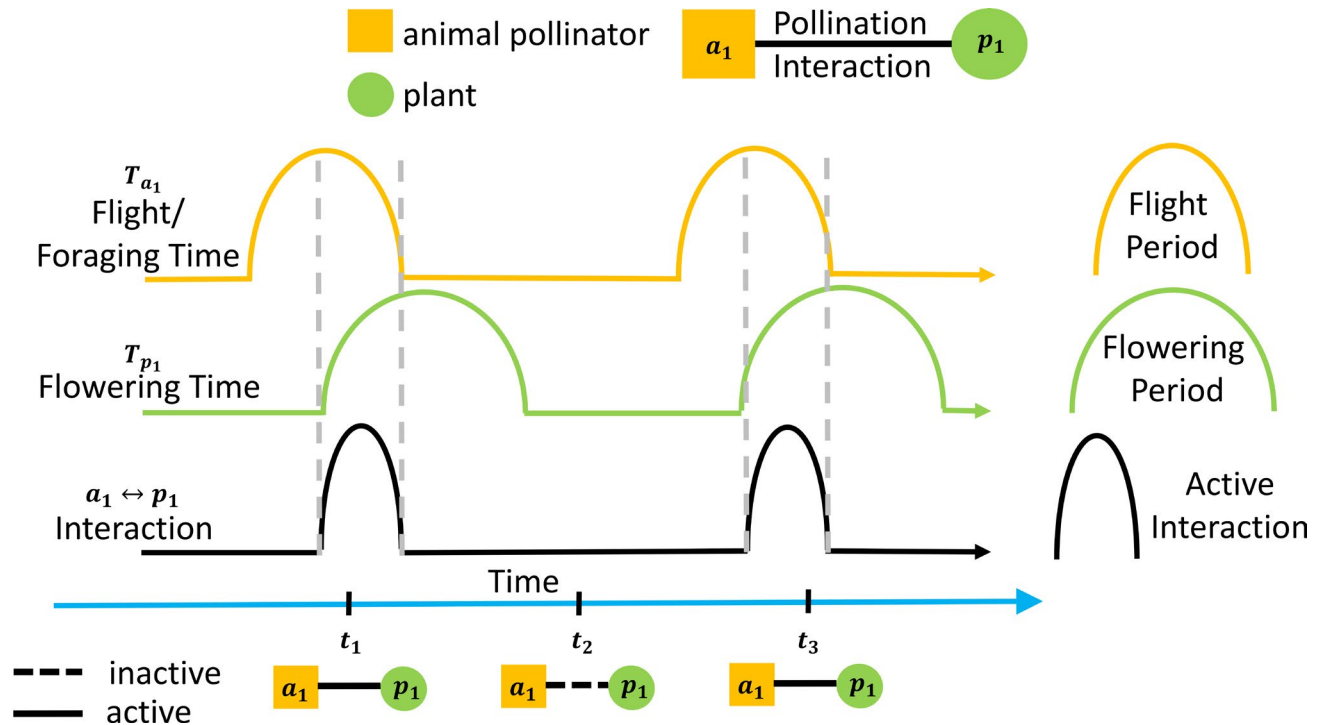
of flowering or foraging, that is, the break periods (see Table S2 and S3; Figure 2, S4 and S5). With these inputs, we created a range of unique plant phenologies through different combinations of durations for flowering periods and interceding non-flowering periods. These combinations created a wide range of flowering overlap among the plant species against which to test our hypothesis (see Figure S12; Appendix S1.8). The quantitative degree of overlap in co-occurring floral resources can be measured in simulations as the total resource overlap (TRO) of the entire plant community, and the average resource overlap (ARO) per plant species by integrating overlapping resource curves ( $R_i$ ) within simulations (Figure S12). See Metrics section and Appendix S1.8 for complete details. In animal pollinators, phenological activity patterns are set-up to produce a range of different flight period lengths separated by differing lengths in between flight periods.

Each flowering (flight) period and intervening period of inactivity between repeating flowering (flight) periods is of equal and constant duration per plant (pollinator) per single simulation. In other words, all plants share flowering period and break period lengths, and all pollinators share flight period lengths per simulation. Spacing on the timeline is as dictated in Appendix S1.3. Additionally, all plants and the inherent phenologies of pollinators and plants do not change within simulations, only between simulations as different phenology parameters are used to create different phenological conditions. Simulations use three fully connected bipartite network frameworks across 2072 combinations of plant and pollinator phenologies to produce 62160 unique networks used to model over 22 million plant-pollinator interactions (see Appendix S1.4).

### Choice of model bee genera and regions for empirical study

The two bee genera *Andrena* and *Lasioglossum* were selected as two contrasting models for this study (Appendix S1.5). They are the two largest bee genera by number of described species (Ascher and Pickering, 2020), and are well-represented in Holarctic bee communities, allowing for comparison across biogeographical regions within and between two distinct lineages each with a shared evolutionary history. Restricting the analysis to two large bee genera controls for potentially confounding effects of phylogenetic position (Resende et al., 2007) while retaining statistical power through the potentially large sample size deriving from the high generic richness. The majority of *Andrena* and *Lasioglossum* species generally lack morphological adaptations for pollen harvesting and therefore favour shallow, open and radially symmetrical flowers, and within each genus have similar dispersal abilities, controlling for the effects of resource accessibility and the cost of travel (see Appendix S1.5 for





**FIGURE 2** Diagram of phenologically mediated pollination interactions. Our model framework simulates pollination interactions over time by controlling key biological rates via phenology functions. Flight/foraging in pollinators is mediated by the function  $T_{a_1}$  and flowering in plants is mediated via the function  $T_{p_1}$ . Foraging and reward production are only active during the flight period and flowering period respectively. The length of these periods and the time interceding each period is set by the user. See Appendix S1.3. Any possible interaction between plants and pollinators is only active during phenological overlap. Otherwise the interaction is inactive in the pollination network

additional detail). However, the genera pursue different life-history strategies, with *Andrena* following a solitary lifecycle with a short foraging period typically lasting a few weeks (Else & Edwards, 2018; Westrich, 1989). *Lasioglossum* species contain a mixture of solitary and social species (Brady et al., 2006), but both types have longer foraging periods, typically lasting several months (Else & Edwards, 2018; Westrich, 1989). *Andrena* and *Lasioglossum* can therefore be considered to have functionally ‘short’ and ‘long’ foraging periods respectively (Appendix S1.7).

*Andrena* and *Lasioglossum* were collected from two biogeographical regions, Britain and Michigan, USA. These regions are both found in the Holarctic and so have broadly similar floral communities composed of the same major botanical families (Stace, 2010; Voss & Reznicek, 2012). Importantly, they differ noticeably in their levels of temporal flowering resource overlap. The highly seasonal continental climate of Michigan (Beck et al., 2018) produces lower degrees of overlap and highly seasonal flowering communities, while the more mild oceanic climate of the British Isles and its consistent temperatures produces longer, overlapping flowering times among plant species (see Appendix S1.6 for additional detail and justification).

Restricting the analysis to the same two bee genera across two biogeographical regions that differ most strongly in their temporal resource overlap rather than

botanical composition, therefore, controls for possible effects of phylogenetic structuring at both the bee and the plant level. This allows us to evaluate the relative importance of foraging period and environmental seasonality in structuring a generalised foraging response in wild bees.

### Selection and standardisation of pollen load data

Pinned *Andrena* and *Lasioglossum* specimens with pollen loads were selected from museum and contemporary non-standardised collections, with the majority (81.9%) collected between 2013 and 2018. Specimens were collected from 265 Michigan sites and 289 UK sites (see Appendix S1.7). Because of the high variability in occurrence between bee species in wild communities in general (Williams et al., 2001) and plant–pollinator networks specifically (Burkle & Alarcón, 2011; Jordano, 2016), capturing an equivalent number of specimens for each species from a similar number of sites within a similar time period is functionally unfeasible for all but the most abundant species. In order to maximise species-level replication and taxonomic representation, an approach favouring the greatest number of samples was adopted without restrictions based on collection locality or date. A total of 2609 suitable specimens from 118 species ( $21.9 \pm 3.8$  samples per species) were analysed,

representing between 30% and 63% of the genus-level fauna of each region. Pollen was removed from specimens and analysed following standard methodology (Wood & Roberts, 2018). Pollen was identified to the lowest possible taxonomic level using light microscopy, in most cases to genus (see Appendix S1.7 for additional detail). A minimum sample size of five pollen loads was selected as the cut-off for inclusion in the study.

## Metrics

Within the model, temporal resource overlap between any two flowering plant species  $p_1$  and  $p_2$  in a simulation is defined as the shared area under their respective resource curves  $R_1$  and  $R_2$  during the simulation. This was quantified as both the sum of all overlap across the entire plant community for TRO and ARO per individual plant species (see Appendix S1.8). Note that resource overlap is not necessarily synonymous with the length of flowering periods. Per unit time, overlap can emerge regardless of flowering period length, so long as flowering periods co-occur in time.

Dietary specialisation was calculated using two metrics, deviation from generalism (DFG) and the coefficient of variation (CV). Both metrics are calculated at the level of pollinator species due to potentially unrepresentative effects of flower constancy that make calculation at an individual level unrepresentative of species-level preference (see Appendix S1.8). When used for simulated pollinators, both metrics take measurement of relative allocation of foraging effort ( $\alpha_{ij}$ ) per pollinator species across all potential resource options as input to produce a per pollinator species dietary specialisation score. The DFG metric is the normalised summation of all pairwise differences of pollinator foraging effort on potential floral resources (Appendix S1.8, Table S4). It ranges from 0 (perfect generalist) to 1 (perfect specialist), regardless of botanical species richness. When used for pollen load data, the quantity of pollen collected from each resource (grouped by either botanical family or botanical genus) is used in place of the foraging effort, under the assumption that greater quantities of pollen collected from any particular plant group correspond to higher foraging effort on that group. Importantly, the algorithm used to calculate our DFG score is a holistic accounting for every possible interaction and compares all possible interactions among each other to accumulate a score. This means that for each bee species, their realised collection patterns are compared to all resources collected by all bees in either the Michigan or UK data sets, therefore geographically partitioning the comparison between regions. Specifically, *Andrena* and *Lasioglossum* (combined) collected from 44 and 37 botanical families in Michigan and the United Kingdom, respectively, and 91 botanical genera in both Michigan and the United Kingdom (see Table S8). We investigate the effects of

organismal phenology and flowering resource overlap by comparing realised collection patterns to all plant taxa in the data set, some of which will only be available during specific time periods and access to which is affected by flight period length.

The DFG metric may not be the best option in all circumstances. It functions best when available data can convincingly represent all possible foraging options, because DFG calculates specialisation considering all potential foraging options. This functions especially well in the model, but it is not necessarily guaranteed in empirical surveys. Therefore, we also employed the CV as our second metric of specialisation (also termed the species specialisation index; Julliard et al., 2006). This well-known summary statistic was applied to our model's output foraging effort ( $\alpha_{ij}$ ) per individual pollinator population, whereas in the empirical data, we take the CV of the percentage of pollen loads collected across plant groups per region (as for DFG). Higher CV values occur with values for specific plant taxa that deviate most strongly from other values, indicating specialisation (Figure S13). As a metric of specialisation, the CV will increase when there are a limited number of extreme values. It performs the same whether or not the full range of possible resource options for foraging pollinators is known and it can function as a means of inter-regional comparison given the similar number of resource options between our sampling regions. The relationship between the two metrics is positive monotonic but non-linear (Figure S13), showing that the two metrics relate to the measurement of specialisation differently as desired. With model results, both DFG and CV were applied to final foraging levels at the end of simulations ( $DFG_{End}$  &  $CV_{End}$ ), as well as to the average foraging levels across the last 1000 time steps ( $DFG_{Avg}$  &  $CV_{Avg}$ ; see Appendix S1.8 for additional details). In contrast, for the empirical pollen load data, metrics were applied categorically by bee genus and region.

## Statistics

Statistical analysis was conducted in R 3.3.2. Regression analysis on model diet breadth results was done using the `lm` function and measured with traditional  $R^2$  metric when working with  $DFG_{End}$  results or with beta regressions (betareg package in R) and the pseudo  $R^2$  metric when working with  $DFG_{Avg}$ . When measuring diet breadth results with  $CV_{End}$  or  $CV_{Avg}$ , log-linked gamma regressions were completed with the `mgcv` package and the amount of deviance accounted for by the regression was measured with the  $D^2$  metric. Due to deeply non-normal data, differences in the metrics generated from the empirical data set were tested using Kruskal–Wallis one-way analysis of variance tests. Confidence intervals in Figure 5 were calculated using the resampling process outlined in the study by Desharnais et al. (2015).

## RESULTS

### Model Results

Our simulation results (Figures 3, 4) support our hypothesis (Figure 1) demonstrating strong effects of temporal resource overlap on the dietary specialisation of pollinators with short but not long flight periods. Figure 3 shows an example of results from one network as an illustration of how resource overlap explains variation in the dietary specialisation of pollinators with shorter flight periods (Figure 3a,c), but does little to explain the dietary specialisation of pollinators with longer flight periods (Figure 3b, d). The different measurable ranges in resource overlap for long flight period bees (Figure 3) stem from the fact that long flight period bees tend to extract more resources than short flight period bees over the course of their full flight period, all else (e.g. resource extraction rates) being roughly equal in the model. This is the case whether overlap is measured in aggregate (TRO) or on average (ARO) due to their strong correlation in our results. The transition from high explanatory power to low explanatory power for temporal resource overlap is apparent as pollinator flight period length increases, regardless of whether specialisation was measured at the end of simulations or averaged across the last 1000 model time steps (visual depiction in Figure 4). This result is consistent across varying lengths of time between pollinator flight periods (i.e. break periods) using either the DFG or CV metric across all networks tested (Figure S14-S16). As predicted, low levels of resource overlap drive pollinators with short flight periods to specialise because potential resource options are limited at any given moment in time. As temporal resource overlap increases, potential options increase resulting in greater generalisation (Figure 3a,c). Bees with long flight periods, on the other hand, do not experience the same limitation of potential options due to temporal resource overlap, because they are active most of the entire flowering season and can potentially access most or all of the flowering plants. Results were consistent regardless of whether resource overlap was measured as TRO or ARO.

### Pollen data results

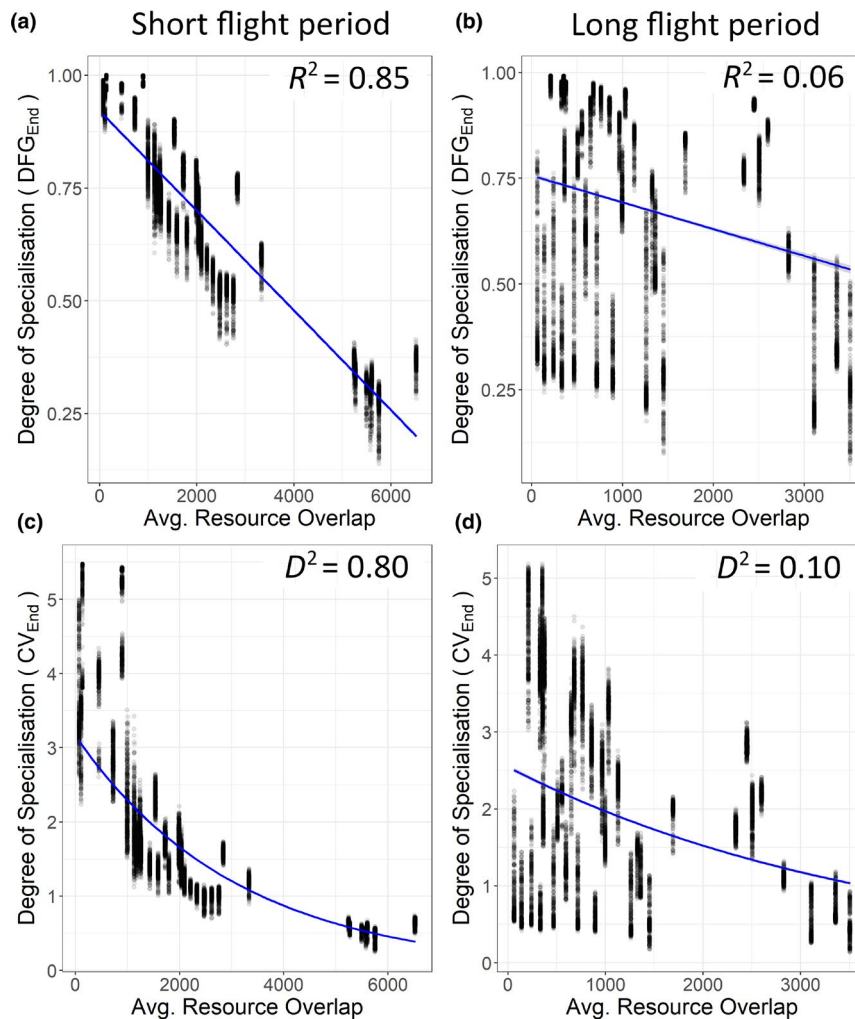
Our empirical results support our hypothesis, showing more specialised diets for bees with short flight periods in more seasonal environments (Michigan) with lower flowering overlap than in less seasonal environments (the United Kingdom) with higher flowering overlap. Additionally, Michigan presents more single family specialists than the United Kingdom (Figure S17). Dietary specialisation between bee genera and regions varied significantly at both the level of botanical family ( $\chi^2 = 30.1$ ,  $p < 0.001$ , Figure 5a) and genus ( $\chi^2 = 27.3$ ,  $p < 0.001$ , Figure 5b). In accordance with our hypothesis, there

was an effect of region at the botanical family level, but only for the short flight period *Andrena* where species in Michigan were significantly more specialised than their British counterparts. In contrast, there were no significant differences for the long flight period *Lasioglossum*. *Lasioglossum* species in the region with lower flowering overlap (MI) were the most generalised of all studied groups, but this difference was non-significant. At the botanical genus level, the same trend was more strongly expressed, as *Andrena* in Michigan were again significantly more specialised than those in Britain, with the latter group showing no differences from *Lasioglossum* in either Michigan or the United Kingdom. Results were consistent when analysed using the DFG metric (Figure S18).

## DISCUSSION

Our model results mechanistically demonstrate how differing phenologies interact with varying degrees of temporal resource overlap to alter pollinator dietary specialisation. Though nominally having the possibility of affecting the realised specialisation of pollinators with both long and short flight periods, increasing temporal resource overlap was only found to increase the dietary generalisation of species with short flight periods. This same qualitative result was found in our empirical pollen load data sets, which presents the first empirical validation of this specific benchmark theory on phenologically mediated adaptive foraging by consumers in general (MacArthur & Pianka, 1966) and pollinators in particular (Waser et al., 1996). In addition to our approach detailed here, regional differences in dietary breadth are also apparent using established analysis methods (Figure S17), and our metrics correlate well with well-known measures (Appendix S1.8), helping corroborate our results.

The lack of a meaningful dietary response by long flight period bees to temporal resource overlap in both the model and empirical data sets suggests that increased temporal resource overlap does not functionally change the resources available to this group. Waser et al. (1996) suggest that longer flowering periods are necessary for long flight period bees to co-occur with a resource and develop a specialised foraging relationship. While long flowering periods may seem intuitively linked to high resource overlap, high resource overlap in and of itself does not necessitate long flowering periods for individual resources. Flowering periods may remain short but overlapped with other resources that are also only available for a short period of time. It therefore follows that the absolute length of the flowering period of individual resources influences specialisation in long flight periods pollinators, but not resource overlap *per se*. In contrast, the absolute length of the flowering period of individual resources is almost irrelevant for short flight periods



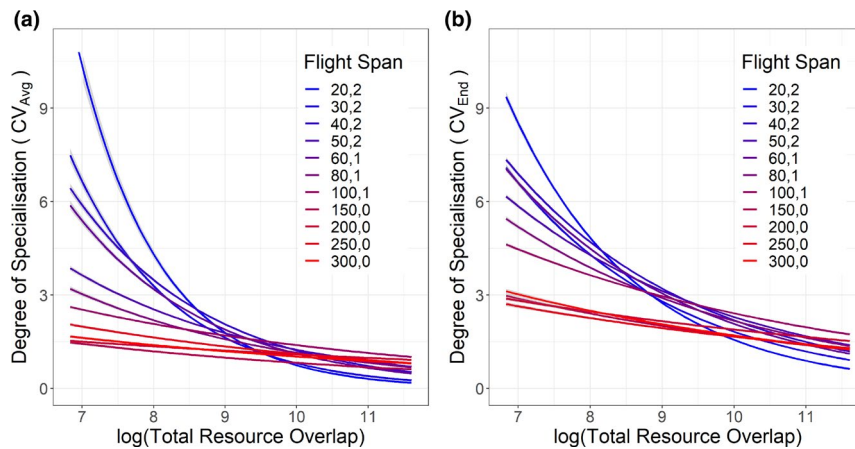
**FIGURE 3** Temporal resource overlap drives specialisation more strongly in short flight period than long flight periods pollinators. Example model output on pollinator specialisation taken across average plant overlap (ARO) for a short flight period (flight period = 20 time steps) and a long flight periods pollinators (flight period = 300 time steps). Each dot represents the dietary specialisation metric of a single pollinator population based on their foraging effort per plant species. Dietary specialisation was measured at the end of simulations using (a) DFG in a short flight period bee,  $\beta = -1.1e^{-4}$ ,  $F$ -statistic:  $1.05e+05$  on 1 and 18498 DF,  $p$ -value:  $<2.2e^{-16}$ , (b) DFG in a long flight period bee,  $\beta = -6.3e^{-5}$ ,  $F$ -statistic: 1089 on 1 and 18498 DF,  $p$ -value:  $<2.2e^{-16}$ , (c) CV in a short flight period bee,  $\beta = 3.2e^{-4}$ , Residual deviance: 671.94 on 18498 degrees of freedom, (d) CV in a long flight period bee,  $\beta = -2.6e^{-4}$ , Residual deviance: 8244.4 on 18498 degrees of freedom. Example data taken from a network framework with 30 plant and 50 pollinator species. Higher values of both DFG and CV metrics indicate higher levels of specialisation while lower values indicate greater generalisation

pollinators because they are active for such a restricted period of time; for them, only the degree of overlap is what determines concurrently available resources.

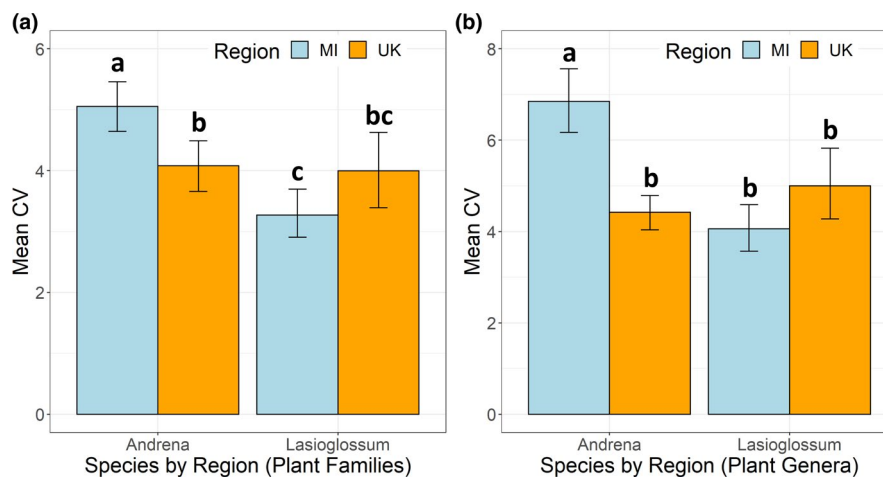
It is important to set these findings within a wider context, specifically that of other known drivers of dietary specialisation. In addition to the impact of spatial and temporal resource density on dietary specialisation, fundamental research (MacArthur & Pianka, 1966; Waser et al., 1996) also points to the constraining impacts of differing resource quality, the cost of travel and morphological limitations (Table 1). These factors are strong enough to shape realised foraging niches. For example, the consumption of certain resources by foraging bees without physiological adaptations is strongly and actively discouraged (Brochu et al., 2020; Wang et al., 2019). Through selecting the regions of the United

Kingdom and Michigan, efforts were made to control for these additional factors in order to focus specifically on and test for the effects of varying bee phenology and flowering period overlap in isolation, *ceteris paribus* (see Appendix S1.5). However, these should not be viewed as mechanisms that explain all aspects of realised dietary breadth in and of themselves. The phenomenon of synchronous specialisation can be commonly observed in many bee communities, where at least two specialists are present at the same time, each specialising on different resources. For example, specialists such as those of *Helianthus* (Asteraceae, *A. helianthi*) and *Solidago/Symphytotrichum* (Asteraceae, *A. asteris*) and those of *Bryonia* (Cucurbitaceae, *A. florea*) and Fabaceae (*A. wilkella*) can be found concurrently in Michigan and the United Kingdom respectively. Clearly, resource





**FIGURE 4** Interactive effect of temporal resource overlap and pollinator flight period on pollinator dietary specialisation. Representative sample of generalised linear models (Gamma distribution with log link functions) showing change in effect of total resource overlap (TRO) on pollinator dietary specialisation in model simulations. Flight period labels indicate the length of the flight period and the number of phenology cycles between subsequent flight periods (see Supplementary Methods). Dietary specialisation is shown as the degree of specialisation measured by the CV of pollinator foraging effort per plant species (a) averaged across the last 1000 time steps and (b) taken at the end of simulations. Higher CV values correspond with a higher level of specialisation while lower CV values indicate greater generalisation. Example data taken from a network framework with 30 plant and 50 pollinator species



**FIGURE 5** Empirical measures of dietary specialisation. Short flight period *Andrena* bees show higher levels of specialisation in highly seasonal (Michigan) compared to the weakly seasonal (the United Kingdom), with no differences for long flight period *Lasioglossum* bees using the CV metric. Moreover, only in Michigan is there a difference in specialisation between the two bee genera, showing a minimal impact of flight period in weakly seasonal environments. Effects are consistent at both the (a) botanical family and (b) botanical genus level. Bars headed by different letters were found to be significantly different via Dunn post hoc test (a):  $p < 0.05$ ,  $DF = 3$ ,  $\eta^2 = 0.21$ , (b): ( $p < 0.05$ ,  $DF = 3$ ,  $\eta^2 = 0.20$ ). Error bars show 95% confidence intervals created via the resampling process outlined in the study by Desharnais et al. (2015)

overlap cannot explain host choice itself where alternative mechanisms relating to morphological or physiological adaptation may be more important (Danforth et al., 2019). Instead, the level of temporal resource overlap should be viewed as a factor that affects the level of realised specialisation across a pollinator community, rather than a predictor of specialisation of the level of the individual species.

It should also be noted that total season length (the overarching flowering season for all flowers) was not investigated in this study. The two regions and selected model genera were specifically chosen to be as similar

as possible, including total season length. It is here that care must be taken. It has long been noted that deserts and arid regions with short and highly concentrated flowering periods play host not only to species-rich bee communities, but also to bee communities that display the highest levels of dietary specialisation anywhere on earth (Danforth et al., 2019; Moldenke, 1979; Waser et al., 1996). The combination of high levels of specialisation occurring during a short flowering period with considerable flowering overlap (and hence many different resources available concurrently) further shows that the explanatory principle of flowering resource overlap

that we demonstrate here cannot be used in and of itself to explain every aspect of dietary specialisation. Instead, total season length (overarching flowering season) may be a third factor affecting opportunities for an individual species to interact with available resources in addition to flight period and flowering overlap. By restricting the resources available outside a narrow flowering window, a short season may result in other factors such as inter-specific competition or morphological and physiological constraints to increase in relative importance despite the high resource overlap. In the future work, the relationships between these three phenological factors and their impact on specialisation could be clarified by leveraging our model's seasonality functions to more explicitly mimic a variety of environmental flowering patterns and interrogate results with relevant empirical data from a wider range of more extreme environments.

With future work in mind, our modelling developments provide a flexible operational basis going forward. We showed that even high-dimension network models can be further expanded to include the dynamics of organisational phenology by focusing on simple inputs and tractability in developing a functional phenology-modelling framework. Our framework provides the adaptability needed to mimic a variety of different biomes' seasonal growth patterns (described above). Additionally, for more direct comparisons to empirical networks in the future, work will need to be done integrating a variety of phenologies among plant and pollinator species in single simulations. While model results matched our theoretical expectations well, empirical results show some signs of complexity. A likely source of this complexity is the fact that pollinator communities exist with many unique phenologies. Expanding the model to study how well the effects of our described mechanism withstand a diversity of phenologies (both at the consumer and resource level) will help to delimit the many factors driving species diet breadth. This is particularly important when diet breadth exists as part of a larger ecological function like pollination or seed dispersal and will indirectly influence diversity and distribution.

Our empirical approach was deliberately regional, and focused on comparing average responses from sampled species in the empirical data set. In adopting this regional approach and using this as a categorical variable, no single bee individual actually experiences these overall regional environmental conditions. The individual bee lives in a subset of the total area and thus is necessarily exposed to conditions that may vary around the regional average. Because this approach gathers together samples from disparate areas across bee species with different habitat specialisations, it is possible that variation in geographic sampling may influence the results. Future empirical studies could focus on specific locations to characterise the degree of floral overlap specific to each site and quantify the dietary breadth of selected taxa through repeated sampling for increased

precision. This would allow an assessment of the degree of variation in dietary specialisation within both regions and individual species, in addition to the comparisons between regions that were made here. However, a more localised sampling strategy is still constrained by the difficulty of standardising measurements (such as analysis of collected pollen from a set number of individuals) across multiple pollinator taxa. Due to their high inherent variability in occurrence (Burkle & Alarcón, 2011; Jordano, 2016; Williams et al., 2001), this would potentially limit the number of taxa that can be compared between sites or regions. The same constraint applies to temporal standardisation. Many pollinator taxa appear sporadically thus limiting the number of individuals and species that can be captured for analysis. Such future studies could test the scalability of the results presented here. In the face of our changing climate, both scalability and range of effect will be important elements in the future investigations involving the phenological drivers of pollinator diets.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### AUTHOR CONTRIBUTIONS

F.S.V. conceived the project. T.J.W., P.G., F.S.V. and J.R.M. developed the conceptual basis for the project. P.G. and F.S.V. developed dynamic model, simulation design, code and dietary specialisation metrics. P.G. implemented simulations and analyses. T.J.W. identified suitable collection sites and bee genera for the empirical study design, collected bee and pollen data, and identified specimens. T.J.W. and P.G. wrote the first draft, and all authors edited and revised the manuscript.

#### CODE AVAILABILITY

Simulation code and simulation data (Figure 3 and Figure 4) are available at the repository: <https://github.com/fsvaldovinos/Phenology>. Phenology parameters used in the simulation portion of our study are available in Table S10.

#### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13884>.

#### DATA AVAILABILITY STATEMENT

Pollen load data (Figure 5) are available as Table S8, and full specimen sampling details are available in Table

S9. Regional flowering overlap data available at: <https://github.com/fsvaldovinos/Phenology>

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